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Direct evidence of megamammal-carnivore interaction decoded from bone marks in historical fossil collections from the pampas region

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The Pleistocene megafauna from South America has traditionally attracted the interest of scientist and the popular media alike. However, ecological interactions among species that inhabited these ecosystems, such as predator-prey relationships or interspecific competition, are poorly understood. To this regard, carnivore marks imprinted over fossil bones of megamammal remains are highly useful to decipher biological activity, including potential interspecific relationships among taxa. In this article, we study historical fossil collections, housed at different European and Argentinean museums that were excavated during 19th and early 20th centuries in the Pampean region, in order to detect carnivore marks over bones of megamammals. Our main goal is to provide crucial information on the ecological relationships of South American taxa during the Pleistocene. Our results indicate that four megamammal long bones of the megafauna from the Pampas region (i.e., families Mylodontidae and Toxodontidae) exhibit carnivore marks. Furthermore, 22 long bones of smaller species and two indeterminate bones present punctures, pits, scores, furrowing and fractures. Members of the large-carnivore guild, such as ursids, canids or even felids, are recognized as the main agents of inflicting the marks. We hypothesize that they represent the last stages of megaherbivores carcasses exploitation, suggesting that multiple taxa were involved in the 'consumption system' of the Pleistocene from the Pampas. Moreover, our observations provide novel insights to further understand past paleoecological relationships of these unique communities of megamammals.

DIRECT EVIDENCE OF MEGAMAMMAL-CARNIVORE INTERACTION DECODED FROM BONE MARKS IN HISTORICAL FOSSIL COLLECTIONS FROM THE PAMPAS REGION

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Abstract

The Pleistocene megafauna from South America has traditionally attracted the interest of scientist and the popular media alike. However, ecological interactions among species that inhabited these ecosystems, such as predator-prey relationships or interspecific competition, are poorly understood. To this regard, carnivore marks imprinted o~~ver~~ fossil bones of megamammal remains are highly useful to decipher biological activity, including potential interspecific relationships among taxa. In this article, we study historical fossil collections, housed at different European and Argentinean museums that were excavated during 19th and early 20th centuries in the Pampean region, in order to detect carnivore marks ~~over~~ bones of megamammals. Our main goal is to provide crucial information on the ecological relationships of South American taxa during the Pleistocene. Our results indicate that four megamammal long bones of the megafauna from the Pampas region (~~i.e.~~, families Mylodontidae and Toxodontidae) exhibit carnivore marks. Furthermore, 22 long bones of smaller species and two indeterminate bones present punctures, pits, scores, furrowing and fractures. Members of the large-carnivore guild, such as ursids, canids or even felids, are recognized as the main agents of inflicting the marks. We hypothesize that they represent the last stages of megaherbivores carcasses exploitation, suggesting that multiple taxa were involved in the 'consumption system' of the Pleistocene from the Pampas. Moreover, our observations provide novel insights to further understand past paleoecological relationships of these unique communities of megamammals.

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Key Words

Museum's collections – Pleistocene - Taphonomy - Pampean Region - Carnivores

Introduction

Reconstructing biological interactions of extinct animals including competition or predator-prey relationships is extremely difficult, and more particularly, when the information available on living analogues is limited (Figueirido, Martin-Serra & Janis, 2016). This is especially the case of ancient South American ecosystems, as members of the megafauna were extinct during the latest Pleistocene-early Holocene, and these groups of mammals have not living counterparts (Cione, Tonni & Soibelzon, 2009; Fariña, Vizcaíno & de Iuliis, 2013). Although Pampean (Argentina) megamammals had traditionally fascinated scientist since 18th century, attempts to understand their paleoecology are much more recent (e.g., Fariña, 1996; Bargo, 2003; Prevosti, Zurita & Carlini, 2005; Prevosti & Vizcaíno, 2006; Figueirido & Soibelzon, 2010; de los Reyes et al., 2013; Fariña, Vizcaíno & de Iuliis, 2013; Scanferla et al., 2013; Soibelzon et al., 2014; Bocherens et al., 2016). To this respect, information of biological activity preserved in fossil remains of megamammals from the Pampean region is always valuable to understand paleoecological relationships among Pleistocene South American communities. As a consequence, carnivore marks preserved in fossil bones of megaherbivores constitute a relevant source of information, as they represent direct evidence of predator-prey relationships, or alternatively, of scavenging activity realized by top predators such are strict flesh-eating and/or bone-cracking hypercarnivores (e.g., Palmqvist et al., 2011; Espigares et al., 2013). Therefore, detecting different marks on bone surfaces of biological activity by means of detailed taphonomic revision using last-generation techniques could provide additional data to understand the paleoecology of Pleistocene communities from the Pampas (Binford, 1981).

Previous studies on bone surfaces made on fossil collections housed in different museums in the Americas have ~~been extremely important, as they have~~ shown carnivore activity, and hence animal interaction (Haynes, 1980; Martín, 2008; Dominato et al., 2011). In South America, evidence of carnivore marks has been reported from different places. Specifically, in the Pampean region, there is a neural apophysis cf. *Eosclerocalyptus lineatus* (Hoplophorini) from the Pliocene (Olavarría) with a clear a carnivore tooth imprint, attributed to *Chapalmalania* (Carnivora; Procyonidae) (de los Reyes et al., 2013). Recently, in the margins of the Salado River a taphocenosis comprising *Hippidion principale* and some indeterminate bones with carnivore marks were associated with *Smilodon* sp. (Scanferla et al., 2013). In the archaeological site Arroyo Seco 2 different bones, among them, extinct species such as *Equus* sp., present carnivore marks (Gutiérrez & Johnson, 2014). In Patagonia *Panthera onca mesembrina* was responsible for interventions involving Mylodontidae and *Hippidion* groups (Martín, 2008), and a member of Felidae produced marks on Gomphotheriidae bones (Labarca et al., 2014) during the late Pleistocene. In Brazil, two sites have been described where *Protocyon troglodytes* scavenged *Notiomastodon platensis, Eremotherium laurillardi* and *Glossotherium* in the late Pleistocene (de Araújo Júnior, de Oliveira Porpino & Paglarelli Bergqvist, 2011), and *Haplomastodon waringi* in the Pleistocene (Dominato et al., 2011).

In this article, we study for the first time different fossil collections recovered from the Pampas region housed in different institutions of Europe and Argentina, and characterized by having megamammal (those mammals > 1000 kg; Cione, Tonni & Soibelzon, 2009) remains. Our main goal is to identify any type of biological activity in order to understand potential relationships between mammalian predators and megaherbivores within South American mammalian communities from the Pleistocene of the Pampas.

Materials & Methods

We studied the following collections: (i) The Rodrigo Botet collection from the *Museo de Ciencias Naturales de Valencia* (MCNV; Spain) is the result of excavations made by Enrique de Carles in the Northeastern Buenos Aires province (Belinchón et al., 2009); (ii) The Dupotet collection, housed in the *Muséum National d' Histoire Naturelle* (MNHN; Paris, France). It belongs to the Pampean age and proceeds from Luján City (Fig. 1); (iii) The Krncsek collection, housed in the *Naturhistorisches Museum of Wien* (NMW; Austria). The collection proceeds from the Luján River in Mercedes City and identified as to “Diluvium - Upper Pampean” (Fig. 1); (iv) Finally, the collection from the *Canal de Conjunción* (La Plata), also housed in the *Museo de La Plata* (MLP). This fossil material was extracted from a 20 m space in the form of a pit near to an old water current (Ameghino in Torcelli, [1889] 1916:128- 129).

These collections were formed during various non-systematic excavations carried out in the eastern region of what is currently Buenos Aires Province, in the Pampas region (Argentina), during the 19th and early 20th centuries. This is an extensive, flat geomorphological unit located in the central area of Argentina. The Quaternary was characterised by loess deposition, with different regressive and transgressive events (Fucks & Deschamps, 2008; Cione, Tonni & Soibelzon, 2009). The early and middle Pleistocene corresponds to the Ensenadan and Bonaerian Stages/Ages that were characterised by a cold and arid environment (Fucks & Deschamps, 2008; Cione, Tonni & Soibelzon, 2009). An important faunal turnover marks the boundary between the two stages, at *ca.* 0.5Ma (Cione, Tonni & Soibelzon, 2009). The late Pleistocene-early Holocene corresponds to the Lujanian Stage/Age. Significant palaeoenvironmental oscillations, eolic pulses, fluvial process and different pedogenetic events influenced this period (Tonni et al., 2003; Fucks & Deschamps, 2008; Cione, Tonni & Soibelzon, 2009). When the collections analysed here were collected, these units were included in the “Pampean Formation” (Tonni, 2011). Current biostratigraphical information (Tonni, 2009) allows locating the material from MCNV to the Ensenadan to Lujanian Stage/Age and the material from MNHN and NMW to Bonaerian and Lujanian Stages/Ages. Furthermore, in the last museum the old reference to Upper Pampean is currently equivalent to the Bonarian Stage/Age (Tonni, 2011) (Fig. 1). The last records of these mammal groups is situated in the Guerrero Member of the Luján Formation deposited between 21.000 to 10.000 BP. (Tonni, 2009). In the case of MLP assemblage, the presence of *Mesotherium cristatum* among the identified species assigns this material to the Ensenadan (Fig. 1) (Cione, Tonni & Soibelzon, 2009).

To understand the natural burial conditions of the remains, we considered different types of bone surface modifications such as post-depositional fractures, the presence of original sediment or concretions, fluvial erosion, trampling, weathering, root growth, manganese spots and burning traces (e.g., Behrensmeyer, 1978; Binford, 1981; Shipman, 1981; Olsen & Shipman, 1988; Lyman, 1994; Fernández-Jalvo & Andrews, 2003).

We followed the literature to identify as carnivore activity a given bone mark (e.g., Haynes, 1980, 1982, 1983; Binford, 1981; Capaldo & Blumenschine, 1994; Lyman, 1994; Domínguez-Rodrigo et al., 2012; Sala & Arsuaga, 2016). As a result, we classified those bone marks that were potentially ~~realized~~ by carnivores in the ~~next~~ categories: (i) *pitting and/or punctures that are produced by the pressure of teeth on bone*: this action can leave a superficial imprint (pitting) or deeper mark (puncture), depending on the level of the pressure exerted and whether this occurs on the softer cancellous bone of the epiphysis or on the harder part of the shaft; (ii) *u-shaped elongated scratches or scores realised when teeth dragged over the surface*: these can be superficial or present as gouges; (iii) *furrowing* is the product of cancellous bone extraction from the epiphyses. Alternatively, this action also can leave a crenulated edge, caused by the border of collapsed bone produced by the bite presenting an irregular edge; and (iv) *spiral fractures* produced by the bone being broken due to pressure from the teeth. Sometimes this action leaves notches in the wall of the bone.

We also made an extensive systematic review of ~~those available~~ actualistic studies describing carnivore marks that different taxa can leave when feeding, and more particularly, recent research on marks made by the members of the large carnivore guild such as ursids (Mammlia, Carnivora, Ursidae), felids (Mammalia, Carnivora, Felidae) and canids (Mammlia, Carnivora, Canidae). ~~Of course~~, specialised bone-breaking hyenas were discarded because they were not present in South America. According to different studies, (i) ursids leave scarce to abundant teeth marks (Haynes, 1980, 1983; Burke, 2013; Saladié et al., 2013; Sala & Arsuaga, 2016). They can crush, furrow, grind and leave crenulated edges (Haynes, 1983; Burke, 2013; Saladié et al., 2013; Arilla et al., 2014); scratches are characterised by short, wide, parallel groups or disordered and superimposed clusters of scratches (Haynes, 1983; Saladié et al., 2013) with U shape or in some cases quadrangular (Saladié et al., 2013). They can also leave elongated gouges (Haynes, 1983; Burke, 2013). Pitting will be planar, flat-bottomed, superficial and circular and they can also fracture bones (Haynes, 1983, 1982). The impression of the teeth will tend to be square or rectangular (Haynes, 1983). In contrast, (ii) felids make fewer marks on the bones since they feed exclusively on meat (Arribas & Palmqvist, 1999; Christiansen & Wroe, 2007; Sala & Arsuaga, 2016). Nevertheless, they can leave important signs of predation (Domínguez-Rodrigo et al., 2012). They can inflict important teeth marks that have an “axe-edge” or elongated V-shape (Haynes, 1983). Their capacity for breaking bones is reduced (Domínguez-Rodrigo et al., 2012; Sala & Arsuaga, 2016), although some groups, such as jaguars, can furrow the epiphyses (Haynes, 1980, 1983; Martín, 2008; Burke, 2013; Domínguez-Rodrigo et al., 2015). Scratches tend to be perpendicular to the long axis of the bone (Haynes, 1983). Finally, (iii) canids can produce a great number of interventions but they not only leave the marks described for the other groups (pitting, punctures, scores, and furrowing) (Haynes, 1983; Domínguez-Rodrigo et al., 2012; Burke, 2013). In contrast, they can also crush and break epiphyses and diaphyses (Haynes, 1982; Yravedra, Lagos & Bárcena, 2011; Sala, Arsuaga & Haynes, 2014; Sala & Arsuaga, 2016). Teeth impressions tend to have a cone or truncated-cone shape (Haynes, 1983). Furthermore, while felids (including *Smilodon*) and ursids have more straight incisive arcades, canids have curved arcades (Biknevicius, Van Valkenburgh & Walker, 1996).

We explore the fossil remains belonging to megaherbivores present in the collections with magnifying glasses of 3.5 X and 12 X. We also used a Dinolite Microscope 4113 model and the software Dinolite 2.0~~, and we took~~ high-resolution digital images using a Panasonic Lumix DMC-TZ35 camera.

For the MLP assemblage we also used the well-established archaeozoological variables such as MNI (Minimum number of individuals) and NISP (Number of Identified Specimens) as they proceed from the same bone assemblage (Lyman, 1994). While the first was used to account for the minimum number of mammals with carnivore marks represented in the sample, we used the second to inform the counting per taxonomic or skeletal part categories.

Results

In total, we studied 1976 bone elements (1478 from the MCNV, 30 from the MNHN, 330 from the MNW, and 138 from MLP). Of them, we only found four bones of megaherbivores with potential carnivore intervention, which represent around 0.2% of the total remains: (i) A right tibia from the MCNV (nº 64-492) that corresponds to cf. Scelidotheriinae gen.; (ii) A left humerus of *Glossotherium robustum* labelled MNHN.F. PAM 119 from the Dupotet Collection housed at the MNHN, (iii) A left distal humerus of *Mylodon robustum* (nº 1908.XI.110) housed at MNW. This specie is ~~currently reclassified as~~ *Glossotherium robustum* (McAfee, 2009); and (iv) At the MLP one distal femur of Toxodontidae (MLP 15-I-20-32). Moreover, in this collection 22 long bones of smaller species and two indeterminate bones have fresh fractures, scratches or punctures. Below, we describe in detail each of the marks identified in the aforementioned remains:

(i) In the right tibia of cf. Scelidotheriinae gen. found at the MCNV the marks are concentrated on the distal epiphysis and medial face, and to a lesser degree, on the proximal epiphysis (Fig. 2). The distal epiphysis has different groups of marks (Fig. 2A). Near the medial edge of the articular face is where most damage is observed. Here, four pits are positioned linearly and surrounded by scores. Posteriorly-anteriorly oriented, the first two pits are smaller with a cuspid-rounded shape (0.3x0.1cm and 0.5x0.2cm) while the other two are bigger and one is semi-rectangular (0.9x0.6cm and 0.5x0.6 cm). On the lateral side of the articular face, a larger transverse score of 2x1 cm was detected. It is next to another pit of 1x0.5cm. Parallel U-shaped scores are located over the metadiaphysis that continue beyond the rim with the four pits (Fig. 2B). They run parallel to the long axis of the bone and surround important furrowing. The results of this action imply that the grooves where muscles such as the *tibia caudalis* and *flexor digitorium longus* were extracted (Fig. 2C). Another important furrow is present on the medial face of the proximal epiphysis (Fig. 2E) that has extracted part of the inner condyle. A crenulated rim surrounds this furrowing, and there are parallel V-shaped teeth marks over the posterior face (Fig. 2C and Fig. 2E). There is one group of five marks in the distal part (1.5x0.4x0.1cm) and two in the proximal part (1.5x0.5x0.1cm), oriented posteriorly-medially. Three thick quadrangular shape grooves were detected over the medial face of the diaphysis (Fig. 2D). One runs along the entire face and is 4.5x1x0.4 cm; the other two are smaller and more superficial, and measure 1.3x1cm and 2x1.3cm. They start at the border of the anterior face and run up to the medial face.

(ii) We detected some marks attributable to carnivores in the distal epiphysis of the left humerus of *Glossotherium robustum* housed at the MNHN (Fig. 3). They are distributed on the articular face, over the condyle and trochlear regions (Fig. 3A). Near the medial side of the trochlear region, there are several punctures of around 0.5 cm in diameter, surrounded by scratches (Fig. 3B). Part of the trochlea has disappeared and there are crenulated edges as a consequence of the furrowing. Over the condyle, at least seven elongated pits of around 1.5x0.7cm were detected (Fig. 3C). Four of these are wide and positioned in parallel. Superficial scratches were also observed. In the border of this region, over the lateral side, are two wide grooves of around 4.5x1cm (Fig. 3D).

(iii) Regarding the left humerus of *Glossotherium robustum* housed at the MNW, over the lateral face of the condyle is a corrugated fracture that encompasses both anterior and posterior faces (Fig. 4A and Fig.4B). The epicondyle was extracted and the border presents a crenulated edge. The collapsed bone is covered with sediment and the rim of the fracture has the same colour as the rest of the bone. Thus the fracture would have occurred before burial. Although the furrowing and crenulated edge is feeble evidence of carnivore intervention (Pickering, Clarke & Moggi-Cecchi, 2004; Domínguez-Rodrigo et al., 2015), the deltoid crest of the posterior face also has a possible 1cm puncture with sediment inside (Fig. 4B). Also in the posterior view, the fractured border is scaled resulting from a pressure exerted on it (Fig.4C and Fig.4D). The regularity of the fracture both on the anterior and posterior faces supports the proposal that the marks on this bone could have resulted from the action of carnivores.

(iv) In the bones of megamammals of the MLP assemblage, a condyle of a distal femur of Toxodontidae with eight elongated and U-shaped scratches was detected (Fig. 5). Five of these are approximately 1.5x0.5cm and the others are 4x0.5cm. In addition, 22 bone shafts from smaller unidentified mammals display spiral fractures. Some of these also present scratches, crenulated edges or light pitting (Fig. 6). Moreover, semi-circular notches were detected. Two indeterminate bones have punctures with a radius of 0.2 and 0.3cm, respectively (Fig. 7). Spiral fractures can be confused with human intervention or can occur naturally (Binford, 1981; Lyman, 1994). Nevertheless, the presence of other typical interventions of carnivores, such as scratches and perforations, enables us to consider them as being produced by carnivore activity. The presence of the Toxodontidae femur and other smaller bones with carnivore marks indicates that a MNI of 2 animals were predated in the location the bones were collected from.

Discussion

The marks are predominant on the diaphyses and epiphyses of long bones. Carnivores generally start to predate the cancellous bone of the epiphyses, since these are easy to penetrate and long bones contain the richest feeding content (Binford, 1981; Blumenschine, 1987; Pickering, Clarke & Moggi-Cecchi, 2004). Two elements correspond to the forelimbs (humeri) and two to the hindlimb (femur and tibia). Both the tibia from MCNV and humerus from the MNHN are elements with combinations of different marks, which reinforces the possibility of a carnivore intervention. The femur from the MLP can be integrated into an assemblage where bones of other mammals have fractures or perforations. This helps the interpretation of this bone and also provides a wider perspective of what could have happened in this case.

The agents: Pleistocene mammalian predators from the Pampas region

Several species of carnivores have been recorded from the Pampas region during the Quaternary. Among ursids, *Arctotherium angustidens* evolved during the Ensenadan Stage/Age. This large 'short-faced' bear was a member of the megafauna as recent estimations of its body mass indicate that the animal exceeded a tonne (Soibelzon et al., 2014). Recent morphometric studies also indicate that this bear probably had an omnivorous diet supplemented by meat or carrion, as dental pathologies detected in some individuals of *Arctotherium* were probably the result of chewing on bones (Figueirido & Soibelzon, 2010). Moreover, Soibelzon et al. (2014) have found biomechanical and isotopic evidence of an omnivorous diet for *A. angustidens* but with scavenging abilities. Other smaller bears that appeared later in South America, including *Arctotherium vetustum*, *Arctotherium bonariense* and *Arctotherium tarijense*, had a more plant-based diet (Figueirido & Soibelzon, 2010).

Three felids were also present in these ecosystems: the saber-toothed cat *Smilodon populator* as the top predator in this region. Its estimated body mass has been calculated as being between 220-360 kg but it could have reached up to 400 kg (Christiansen & Harris, 2006). This sabre-toothed cat could even have been capable of hunting on juvenile *Megatherium americanum* (Megatheriidae) with a body mass of adult individuals ranging between 4 and 6 tonnes (Prevosti & Vizcaíno, 2006; Bocherens et al., 2016). However, its large saber-like canines that were used to attack to the throat of their prey (Antón et al., 2004) precluded *Smilodon* for breaking or consuming bones regularly, although they could have inflicted some damage during soft-tissues consumption (Arribas & Palmqvist, 1999; Van Valkeburgh & Hertel, 1993; Binder & Van Valkenburgh, 2010). The other two hypercarnivorous felids were *Puma concolor* with an estimated body mass of 47/50 kg (Christiansen & Harris, 2006; Prevosti & Vizcaíno, 2006) and *Panthera onca* weighing *ca.* 120 kg (Prevosti & Vizcaíno, 2006). Although these species would have fed on prey of *ca*. 600 kg, occasionally they could prey upon juvenile megamammals (Prevosti &Vizcaíno, 2006). Pumas usually do not consume bone, but *Panthera onca* is potentially able to broke and consume it (Martín, 2008; Muñoz et al., 2008; Domínguez-Rodrigo et al., 2015).

The hypercarnivorous canids were also present in these ecosystems at that time. They could have cooperated in order to hunt large mammals and juvenile megamammals, and they also had scavenging capabilities. This may have been the case of *Theriodictis platensis*, weighing *ca*. 37 kg, which evolved during the Ensenadan Stage/Age. It could have preyed upon animals of around 600 kg or even upon animals of extreme age classes (i.e., very old and juvenile individuals) or upon pathological members of the megafauna (Prevosti & Palmqvist, 2001). During the Pleistocene, there were different species of *Protocyon*, weighing between 20 and 25 kg. These could have scavenged carcasses of megamammals, and even may have competed with *Smilodon populator* (Prevosti, Zurita & Carlini, 2005; Prevosti & Schubert, 2013; Bocherens et al., 2016).

Therefore, carnivores with an important capacity for bone modification would have produced the different interventions described. Accordingly, felids such as *Smilodon* or *Puma* must be dismissed, due to their reduced bone-damaging capacity. In order to get an idea of which of the remaining carnivores could have participated in inflicting the marks we briefly describe each bone:

The MCNV's cf. Scelidotherinae gen. tibia is the bone that presents the most important carnivore interventions. A combination of pitting, scratches and important furrowing, both on epiphyses and medial faces, was observed. Even though the three groups of carnivores can leave these types of marks, some characteristic allows relating the damage described to ursids. The group of aligned pits imprinted on the medial rim (Fig. 2A) of the distal epiphysis are planar, flat-bottomed and have a semi-rectangular shape that could have been made by premolars or molars as mentioned for this group (Haynes, 1983). While the V-shaped parallel teeth marks observed on the posterior face (Fig. 2C and Fig. 2E) could be related to a series of incisors and canines and would coincide with the dragging action of a straight incisor arcade (Biknevicius, Van Valkenburgh & Walker, 1996). On the other side the parallel scores as the ones seen in the distal metadiaphysis (Fig. 2B) are generally a type of damage adjudicated to this type of animal (Haynes, 1983; Saladié et al., 2013). Also, the intensive furrowing coincides with the bone-breaking capacity of this animal (Soibelzon et al., 2014). Other damage indicated for ursids and observed in the tibia is the elongated gouge as seen in the lateral side of the articular face (Fig. 2A) or the quadrangular shape grooves of the medial face of the diaphysis (Fig. 2D) (Burke, 2013; Saladié et al., 2013). These ones and the gouges observed in the distal metadiaphysis do not have regular walls and bottoms, as indicated for ursids (Saladié et al., 2013). Nevertheless, according to current research, they must be superficial, a feature not observed for these marks (Haynes, 1983; Saladié et al., 2013). Consequently, it cannot be discarded that more than one animal participated in imprinting the complex and variable types of marks registered in this tibia. To this respect, some authors suggest that damage produced by ursids is slight in comparison with other groups (Haynes, 1983; Arilla et al., 2014; Sala & Arsuaga, 2016) a pattern not observed here. In this sense, it cannot be discarded that *Panthera onca* could have also been involved. They also possessed straight incisive arcades (Biknevicius, Van Valkenburgh & Walker, 1996) that could have produced the elongated V-shape marks (Haynes, 1983) of the posterior face. The important furrowing noticed in both ends of the bone also matches with their capacity of realizing this type of damage (Martín, 2008; Domínguez-Rodrigo et al., 2015). The humerus of *Glossotherium robustum* housed in the MNHN has less bone loss than the tibia. This element also presents several characteristics that can be related to *Arctotherium*. As notice for the tibia, the short and wide scratches present in the condyle and the wide and elongated and superficial pitting, coincides with actualistic studies on ursid marks (Haynes, 1983; Burke, 2013; Saladié et al., 2013). Nevertheless, the presence of punctures in the trochlea, also characteristic of felids, means that other options, such as *Panthera onca,* cannot be disregarded (Haynes, 1983). Both groups also can furrow the epiphysis (Martín, 2008; Arilla et al., 2014; Domínguez-Rodrigo et al., 2015) as observed for the trocheal part of the bone.

The furrowing on the MNW's *Glossotherium robustum* humerus is less clear than for the other two cases, since different animals could have inflicted this type of cancellous extraction. The cusp that made the associated puncture could be related to secodont teeth, such as felids or canids. Both have the capacity to extract cancellous tissue, although canids leave fewer marks in mammals larger than 400 kg (Yravedra, Lagos & Bárcena, 2011). Patagonian sites with important furrowing in Mylodontidae bones attributed to *Panthera onca mesembrina* (Martín, 2008) could be an antecedent when considering the types of marks that jaguars can make on the limbs, as observed in this case.

The marked femur of Toxodontidae from the MLP has to be integrated with the other evidence in order to interpret which carnivore was involved. Of the taxonomic groups represented by the 138 bones reviewed, 62.32% (NISP: 86) belong to indeterminate species, while the remaining 37.68% (NISP: 52) were identified at a general level. Among them, equids form the most important group, accounting for 36.53% (NISP: 19) of the identified elements. Megamammal bones are the second most widely represented group, at 30.76% (NISP: 16). Appendicular skeletal elements (73.92% or NISP: 102) composed predominantly the assemblage. Axial and planar bones contribute only 13.77% (NISP: 19) of the assemblage and indeterminate fragments account for 12.31% (NISP: 17). Of these carnivore-marked bones, 81.48% (NISP: 22) are indeterminate diaphyses of the long bones mentioned above, coinciding with the general abundance of appendicular skeletal elements. The dominance of long bone elements and the null or scarce importance of axial parts could have resulted, in part, from carnivore activities that transported some limbs to this area. The carnivore/s involved in the formation of this assemblage must have had the capacity to break long bones and/or the ability to predate megamammals. In this sense, given the absence of specialised bone-crushers in the Americas, some type of canid could have been responsible for this type of assemblage. Therefore, either *Theriodictis platensis* or *Protocyon scagliorum* from the Ensenadan Stage/ Age could have been responsible for these marks, as seen in the Brazilian cases (de Araújo Júnior, de Oliveira Porpino & Paglarelli Bergqvist, 2011; Dominato et al., 2011).

Megamammals carcass exploitation during the Pleistocene

Although discussing how these animals were predated is difficult without more contextual information, taking into account the skeletal elements and location of marks (i), and the level of use of the bones (ii), it seems most likely that these marks represents the last stages of consumption of megamammal carcasses.

(i) Marks on the tibia and the humeri are situated on the epiphysis, both the articular surface and metadiaphyses. In a hunting event, carnivores that have access to a large mammal usually begin to feed on the abdominal part, then moving to femoral muscle masses, leaving some marks on the distal epiphyses and diaphyses (Haynes & Klimowicz, 2015). Thus, the initial consumers feed on viscera and muscles, inflicting few damage to bones (Haynes, 1982; Blumenschine, 1986; Arribas & Palmqvist, 1999; White & Driedrich, 2012; Haynes & Klimowicz, 2015). Forelimbs are usually consumed later, since the skin is harder in these areas (Haynes, 1982; Haynes & Klimowicz, 2015). The same usually happens with lower limb bones, such as the tibia, due to the smaller quantity of the meat they have (Haynes, 1982, Blumenschine, 1986; Haynes & Klimowicz, 2015). The intense gnawing of the cf. Scelidotherinae gen. tibia, both on the distal epiphysis and medial face of the diaphysis, as well as to a lesser degree on the proximal epiphysis, implies that this element was fully exploited. This is not expected in the case of an early access event, where other more nutritious parts of the carcass are available. The presence of marks on the diaphysis indicates that even the hardest part of the shaft was utilised. The same is true for both *Glossotherium robustum* humeri. The damage to the distal epiphyses was inflicted in subsequent stages and not in a first access event (Haynes, 1982). The presence of furrowing on the three elements implies that the various carnivores involved were consuming a substantial amount of bone. In the case of the MLP assemblage, the dominance of broken diaphyses of long bones indicates the need to access the marrow. The use of the medullar cavity is related to secondary access to the carcass (Binford, 1981; Haynes, 1982; Blumenschine, 1987; Arribas & Palmqvist, 1999; Capaldo & Blumenschine, 1994; Sala & Arsuaga, 2016).

(ii) Intensity of use of a carcass is related to resource availability (Haynes, 1980, 1982), pack hunting size group (Van Valkenburgh et al., 2016) or the quantity of different carnivores that can access to a carcass. In general terms, large animals usually conserve tissues for longer after dead (Blumenschine, 1987) and have fewer marks than smaller ones (Domínguez-Rodrigo et al., 2015). As the meat is ~~feed~~, carnivores will tend to attack the remaining carrion (Binford, 1981; Haynes, 1982; Blumenschine, 1986; White & Driedrich, 2012; Haynes & Klimowicz, 2015, Sala & Arsuaga, 2016) and more significant marks on bones are inflicted. Thus, marks on articulation surfaces could indicate that by the scavenging time, the bone holds small amount of meat, since this is consumed in a first access event. This would be the case of the cf. Scelidotherinae gen. tibia from the MCNV, the *Glossotherium robustum* left humerus from the MNHN and the Toxodontidae femur from the MLP (along with other broken bones). The same hypothesis can be made for the *Glossotherium robustum* humerus from the MNW, although in this case, a lack of marks on the articulation surface could indicate that the bone was still attached to the rest of the limb. In general, the intensity of the marks and fractures observed indicates advanced stages of modification (Haynes, 1982; Sala & Arsuaga, 2016). This contradicts the hypothesis that they could have been made in an early first access event.

According to the described bones, during the Pleistocene, different species of the large carnivore guild would have access and consume megamammals' bones and/or marrow of smaller animals thus representing the last stages of a consumption sequence. One possible scenario is that after their death, different carnivores would have consumed the primary edible tissues of the bony elements presented here. In a next stage, exploitation of the bones and marrow would have occurred. It is in this stage that tooth marks, furrowing, and bone cracking would have been done. Such a situation in the Pampean region, would had imply different carnivores could have fed on a single carcass as was recorded in European and African sites (Binford, 1981; Blumenschine, 1987; Arribas & Palmqvist, 1999; Pickering, Clarke & Moggi-Cecchi, 2004; White & Driedrich, 2012; Haynes & Klimowicz, 2015; among others).

In a broad carnivore-herbivore interaction level, in the Pampean region, other carnivores or even avifauna would have probable exploited this megamammal community. To this respect, *Canis* *nehringui* was present during the late Pleistocene-early Holocene and although it would have fed on medium size mammals, exploitation of bigger species could have been possible (Prevosti & Vizcaíno, 2006). Also a diversified Pampean avifauna existed during Pleistocene-Holocene times that included condor-like vultures, such as *Geronogyps reliquus*, *Sarcoramphus papa* and *Vultur gryphus*, as well as also vultures like *Coragyps atratus,* and at least two types of large falconids identified at generic level as *Caracara* sp. The rich megafauna would have provided an important source of food for these species (Tonni & Noriega, 1998; Noriega & Areta, 2005; Cenizo, Angolin & Pomi, 2015; Jones et al., 2015), so their participation in the Pampean ecosystems from the past cannot be disregarded. At the end of the Pleistocene also *Homo sapiens* has to be added to this complex scavenging niche (Borrero & Martín, 2012). Nevertheless, ~~he~~ also created new predation opportunities, through hunting these animals in a more successful way than existing carnivores (Cione, Tonni & Soibelzon, 2009). The inclusion of them suggest that megamammals' exploitation would have developed in a competitive interspecies context in the Pleistocene of this region (Prevosti, Zurita & Carlini, 2005; Prevosti & Vizcaíno, 2006; Bocherens et al., 2016). In this sense, it was recently pointed that Pleistocene communities had more hypercarnivore species than extant communities given the abundance of megaherbivores and consequently competition for the carcasses would have been intense (Van Valkenburgh et al., 2016).

Although little can be said about the acquisition way of the bones described here, it seems likely that predator-prey relationships and/or scavenging activities would have been extensively developed given the richness of Pampean megamammals communities (Cione, Tonni & Soibelzon, 2009). Megamammals, as it is true today of megaherbivores, have few natural predators (Owen-Smith & Mills, 2008; Fariña, Vizcaíno & de Iuliis, 2013), although it cannot be discarded that Pleistocene hipercarnivorous species would have occasionally pack-hunting adult individuals and confront juveniles ones (Van Valkenburgh et al., 2016). Natural diseases and paleoenvironmental stressors would have also influenced in mortality and would have acted as top-down pressures stimulating the interspecific competition for the carcasses.

Conclusions

Four megaherbivore fossil bones, 22 bones of smaller species, and two indeterminate bones with carnivore marks were found in different paleontological collections. These remains were collected from the Pleistocene of the Pampas region. Here, we conclude that megaherbivores were a considerable resource exploited through Pampean Pleistocene ecosystems. After a first access event, the remaining carrion would have been used by a diverse spectrum of carnivores. Especially the marks described predominates on bones of the appendicular skeleton that are the richest part with regard to both tissue and fat content, particularly the epiphyses which are the easiest to penetrate (Binford, 1981; Pickering, Clarke & Moggi-Cecchi, 2004). In the material presented here, ursids, canids and possibly felids would have consumed the residual tissue, inflicting different types of teeth marks, including pits, punctures and scratches, furrowing bone epiphyses, and even breaking the diaphyses of long bones in order to access the marrow. They represent the last stages of carcasses exploitation. This situation suggests the participation of a diverse array of carnivores that consumed all the edible tissues plus bony elements and consequently the development of competitive interspecific interactions for this resource.

Although the sample is small, it increases significantly our knowledge of the past paleoecological relationships in the region. At a broad level, considering the time-span and the different species involved, megaherbivores would have implied an important resource for different member of the large carnivore guild of this region. The exploitation of this resource has occurred at least since the Pliocene (de los Reyes et al., 2013) and continued throughout the Pleistocene according to the evidence presented here. This long term-span situation matches with recent proposals that the maintenance of Pleistocene large mammal’s communities was part of a stable composition developed over the last 1 million years. The development of different trophic levels and multiple competitive species would have allowed them to persist across time and overcoming different paleoclimatical fluctuation. This situation lasted until late Pleistocene-early Holocene times when most of the megafaunal extinction occurred (Van Valkenburgh et al., 2016).

Current taphonomical knowledge allows analysing these old collections to obtain new results and offers new insights to develop future field systematic fieldwork. The application of both lines of research will provide crucial information regarding the evolution of past Pleistocene ecosystems of the South American Southern Cone.

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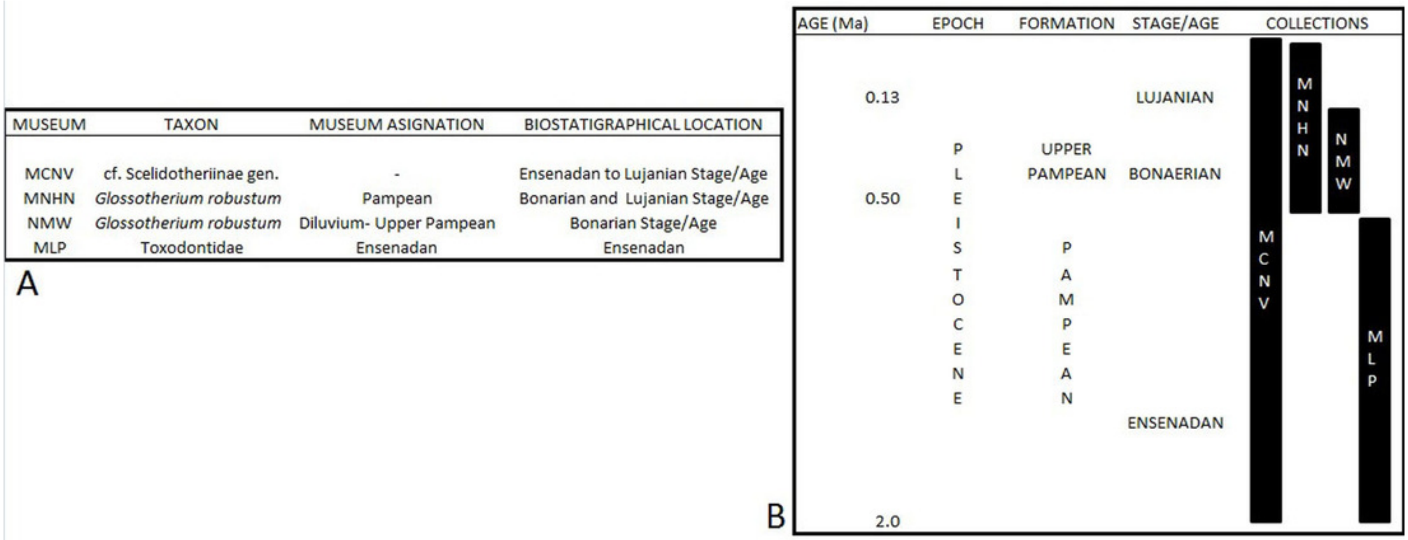
Figure 1

Figure 1.

Taphonomical and stratigraphic context. A) Determination of megamammals’ bones according to the museums assignation and current biostatigraphical determination. B) Pleistocene Formations, Stage/Age (out of scale) and the approximate time loc



MUSEUM	TAXON	MUSEUM ASIGNATION	BIOSTATIGRAPHICAL LOCATION
MCNV	cf. Scelidotheriinae gen.	-	Ensenadan to Lujanian Stage/Age
MNHN	*Glossotherium robustum*	Pampean	Bonarian and Lujanian Stage/Age
NMW	*Glossotherium robustum*	Diluvium- Upper Pampean	Bonarian Stage/Age
MLP	Toxodontidae	Ensenadan	Ensenadan

Figure 2

Figure 2

Right tibia of cf. Scelidotherinae gen.,64-492 from MCNV, posterior-medial view, indicating the different marks described in the text: A) distal epiphysis, the rectangle and zoom indicate the four linearly-positioned pits; B) metadiaphysis with the U-shaped parallel scores circled; C) furrowing of the distal metadiaphysis, with a circle indicating V-shaped parallel teeth marks on the posterior face; D) medial face of the diaphysis with a magnified image of one of the three thick grooves; E) furrowing of the proximal metadiaphysis.

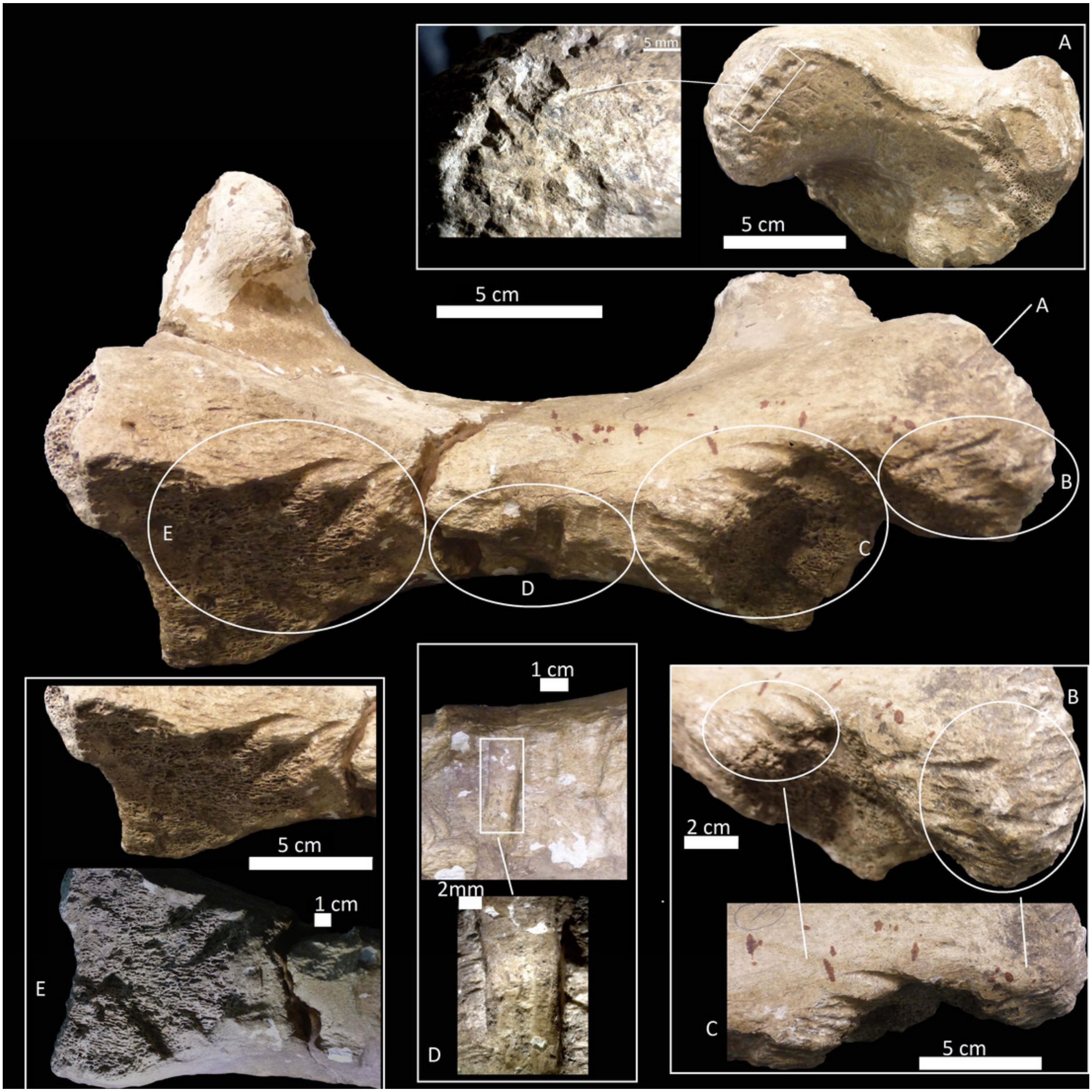

5 mm
A
5 cm
5 cm
A
B
E
D
C
1 cm
B
5 cm
2 cm
1 cm
E
2mm
D
C
5 cm

Figure 3

Figure 3

Left humerus *Glossotherium robustum*, MNHN.F.PAM 119 from MNHN, anterior view, indicating the different marks described in the text: A) front view of distal articular face; B) amplification of trochlear region where punctures and scratches were detected; C) amplification of condyle with pits; D) thick grooves on the lateral face.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

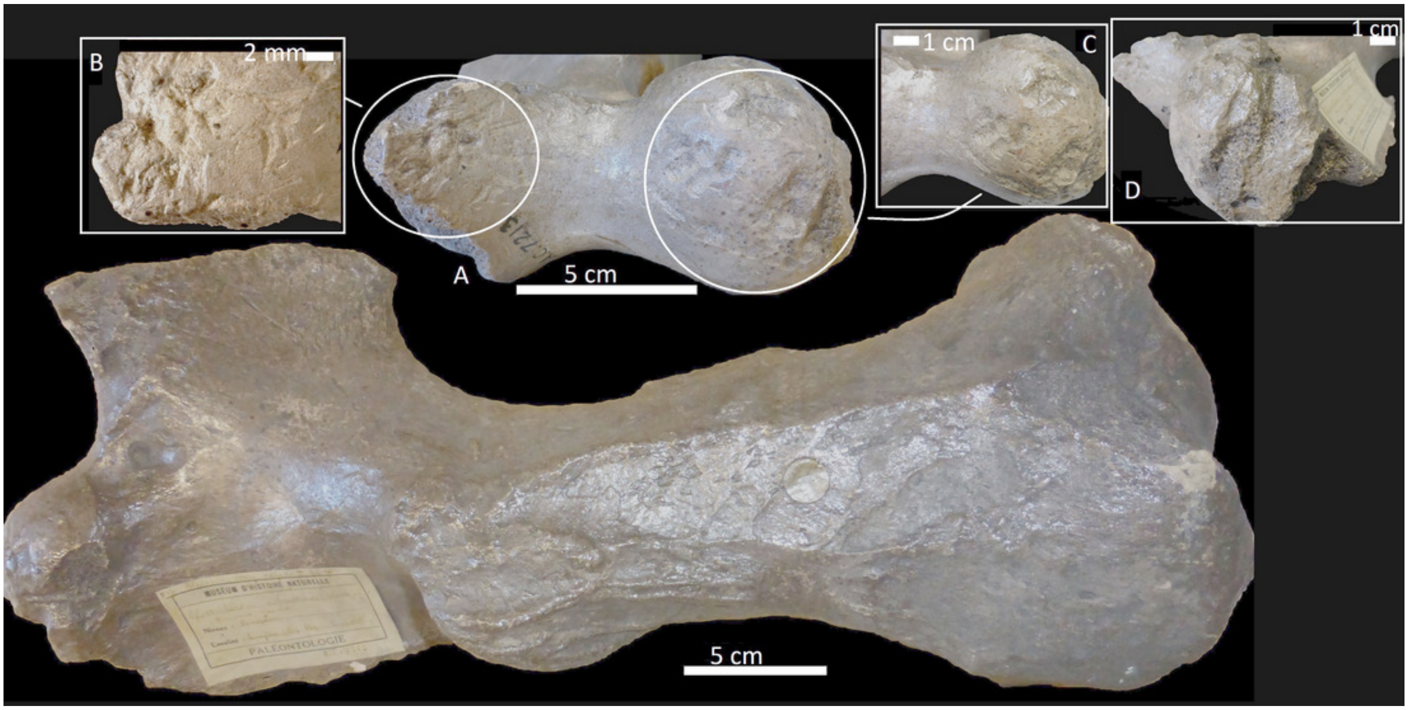


Figure 4

Figure 4

Left distal humerus of *Glossotherium robustum*, 1908. XI.110 from MNW: A) anterior face; B) posterior face, indicating the puncture; C) amplification of the posterior rim; and D) indication of the scaled border.

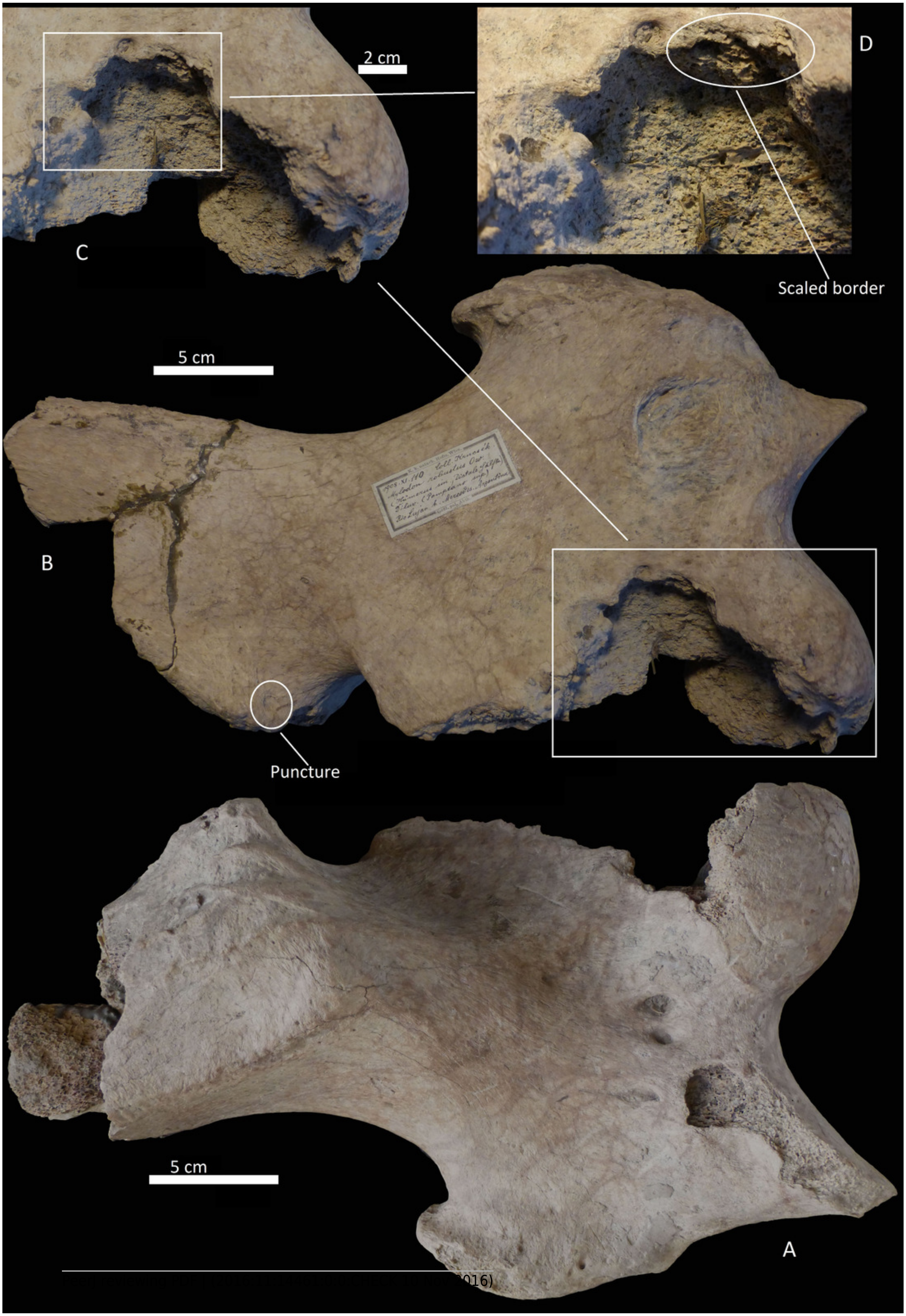

2 cm
D
C
Scaled border
5 cm
B
Puncture
5 cm
A

Figure 5

Figure 5

Condyle of the distal femur of Toxodontidae, 15-I-20-32 with elongated and U-shaped scratches.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

Figure 6

Figure 6

Bone shafts with spiral fracturing. From top to bottom: MLP 15-I-20-33, MLP 15-I-20-34, MLP 15-I-20-35.

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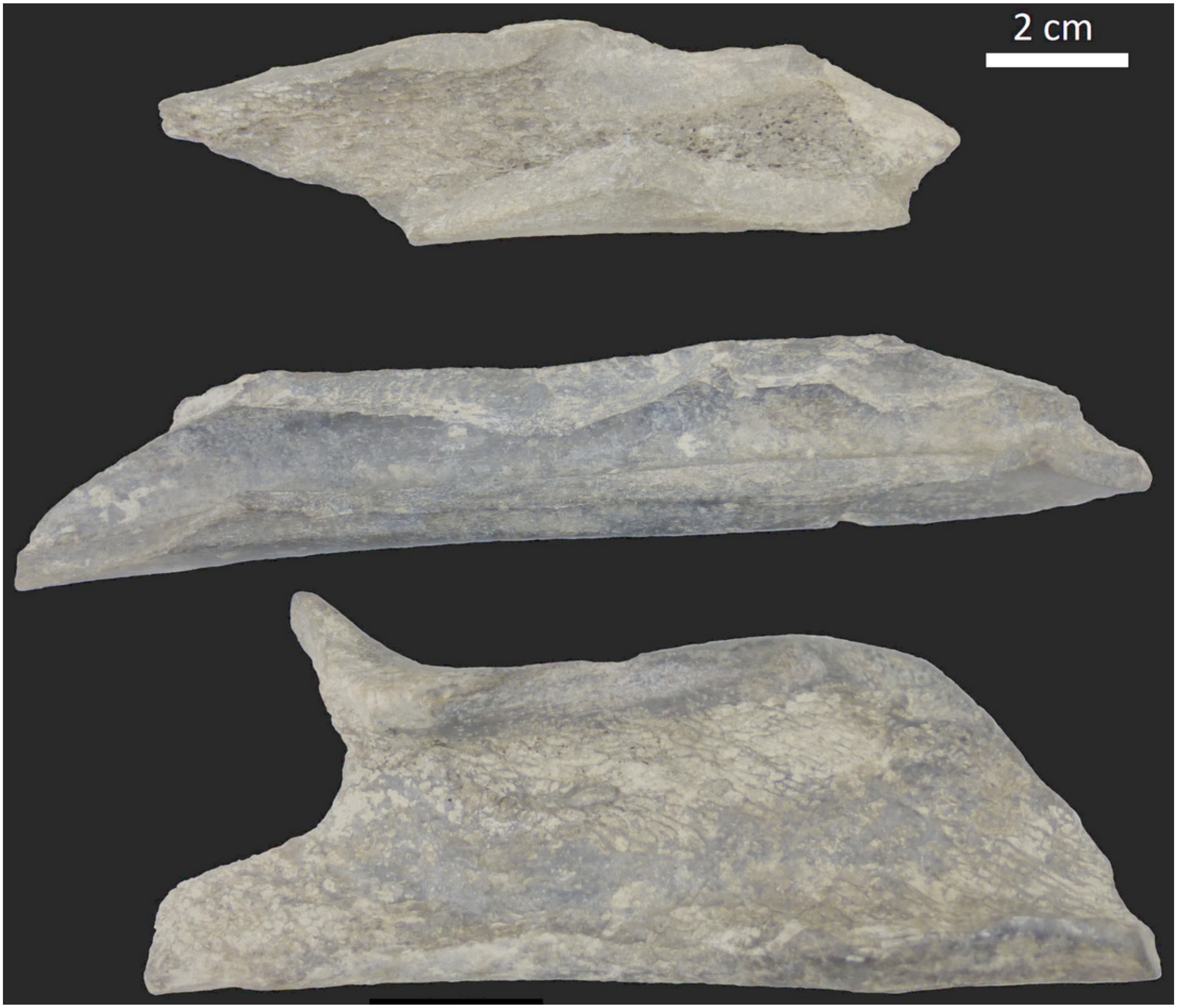

Figure 7

Figure 7

Indeterminate fragment of bone, MLP 15-I-20-36 with perforation.

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